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Stolonophora, A New Genus of Geocalycaceae¹

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There are three well-defined subfamilies within the Geocalycaceae, i.e., subf. Lophocoleoideae, subf. Geocalycoideae and subf. Leptoscyphoideae (see Schuster and Engel, 1973). The genus *Stolonophora* Engel & Schust., new genus, belongs to subf. Lophocoleoideae, which is characterized by possessing perianths with three ± equally developed lobes of which the third is ventral in position.

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Stolonophora Engel & Schust., new genus

Plantae dioicae, erectae, virides vel brunneolae. Ramifications semper fere intercalares, rami typi ventricalis atque lateralis, rami terminales rarissimi, typi *Frullaniae*; stolones frequentes, prostrati vel descendentes. Cortex caulinus e cellulis admodum incrassatis efformatus. Folia transverse vel subsuccube disposita, concava, oblata vel rotundata vel ovata, apice et margine integris. Cellulae foliorum leviter vel manifeste crassi-tunicatae, trigonis mediocribus vel magnis; cellulis dimorphis, plerumque 2 (raro 3) guttis olei praeditis, paucis guttula destitutis. Amphigastria manifesta, deminuta, 0.15-0.55× latitudine caulinis, indivisa vel bifida. Gemmae nullae. Androecia intercalaria vel terminalia ad axillas foliacias longas; antheridia solitaria, pedicellus uniseriatus vel hic inde biseriatus. Gynoecia ad axillas foliacias

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longas; bracteae integrae, bracteolae admodum deminutae, bifidae vel indivisae. Perianthia trigona, clavata vel \pm campanulata, ore integro. Capsula pariete 3-4-stratoso instructa. Sporae 14-17 μ ; elateres 7-8(-9) μ lati, bispirales.

Typus.-*Leioscyphus* (?) *abnormis* Besch. & Mass. Bull. Mens. Soc. Linn. Paris 1: 629. 1886.

Plants caespitose; erect, axes 0.8-10.5 cm. tall, leafy shoots 0.5-1.2 mm. wide; green to yellow-brown to red-brown to brown.

Branches nearly exclusively ventral- and lateral-intercalary, terminal branching very rare, of *Frullania* type, leafy branches erect; stolons present, prostrate or descending, often branched, often originating near base of microphyllous or leafless erect axis that soon becomes leafy.

Stems \pm rigid or wiry, 8-11 cells in diameter, cortex in 1-2 rows of very thick-walled cells the same size as or smaller than the medullary; medullary cells thin to slightly thick walled. Rhizoids on leafy axes few or none, restricted to lower underleaf bases; on stoloniform axes at bases of both leaves and underleaves.

Leaves transverse to subsuccubously oriented, insertion narrow, transverse to distinctly succubous, leaves commonly subvertical, entire leaf weakly to moderately concave or moderately concave in median portions with the peripheral portions nearly flat; oblate to rotundate to ovate; apices undivided, entire; margins entire, broadly rounded, dorsal margin rather long decurrent.

Leaf cells with walls slightly to distinctly thickened, trigones medium to large; cuticle smooth or finely papillose. Cells dimorphic: a majority with 2(-3) oil-bodies per cell, 10-20 per cent of cells without oil-bodies; oil-bodies colorless, faintly granulate, subspherical to ovoid.

Underleaves reduced, \pm appressed to moderately spreading, hard to discern, 0.15-0.55 \times the stem width; undivided or bifid and with segments cilialike; lamina margins entire or with 1 tooth.

Gemmae absent.

Plants dioecious; androecia intercalary or (at first) terminal on main axis or long leafy branches; bracts subequal to or somewhat smaller than leaves, ovate to rotundate, free margin of saccate portion entire or with 1 slime papilla or with 1-2 teeth, bracts otherwise entire; antheridia solitary, stalk uniseriate throughout or with isolated cells vertically septate.

Gynoecia on main axis or long intercalary branches; subfloral innovations absent or from axil of bract of innermost series or bract or bracteole of second series, innovations often repeatedly producing perianths. Bracts becoming progressively larger toward the perianth; bracts of innermost series deeply concave in median basal portion, rotundate to subrectangular to obovate; apices undivided, entire; margins entire. Bracteoles of innermost series free from bracts; highly reduced, hardly modified from underleaves; very short bifid or undivided; lamina margins entire or with several slime papillae and 1 to several small teeth. Perianth trigonous, clavate to \pm campanulate, somewhat or hardly laterally compressed, ventral lobe convex to somewhat infolded; perianth expanding or \pm contracted toward the mouth; the mouth \pm 3-lobed, entire.

Seta 7-9 cells in diameter, with 25-32 rows of outer cells surrounding an inner core of cells smaller, subequal or slightly larger than outer row. Capsule wall of 3-4

layers, outer layer of cells 2.2-3.7 \times as thick as each of interior strata, outer layer with red-brown thickenings on radial walls, the thickenings wide nodulelike to wide spinelike, semiannular bands sparing or absent, exposed wall thickened; intermediate and inner layers of cells subequal in thickness, intermediate layer(s) with thickenings on radial walls, but often considerably tangentially dilated; inner layer of cells with incomplete semiannular bands extending for varying lengths, bands occasionally complete, nodulose and sharp spinose thickenings common. Spores 12-17 μ , light brown, exine with short, close vermiculate ridges. Elaters 7-10 μ wide, bispiral to 2-3-spiral.

One of the two species here placed into *Stolonophora* has been previously assigned to *Clasmatocolea* (Grolle, 1960), and the other species has been treated as a synonym of a *Clasmatocolea* taxon (Grolle, 1972). The following ensemble of features will distinguish *Stolonophora* from the genus *Clasmatocolea*: a) the presence of stolons; b) the nearly exclusively intercalary branching (only a single terminal, *Frullania*-type branch was observed); c) the erect growth; d) the dimorphic leaf cells, with the majority possessing oil bodies, but with 10-20 per cent of the cells lacking them (see fig. 5); and e) the vertically oriented, subtransverse leaves.

Rather than possessing affinities with *Clasmatocolea*, it seems more likely that *Stolonophora* is closer to the purely Austral complex centering around *Pachyglossa* and *Lophocolea boveana* of southern South America, and the *L. australis-gunniana* complex of South America-New Zealand-Tasmania. The relationships of *Stolonophora* to the New Zealand taxa *Pachyglossa tenacifolia* and *Lophocolea gunniana* seem particularly pertinent. In both of the latter taxa, as well as in *Stolonophora perssonii*, we find the leaf cells are clearly dimorphic, with a varying percentage devoid of oil-bodies, others bearing typically one or two, rarely three, finely botryoidal oil-bodies of, basically, identical form. Although this similarity may be fortuitous, it is linked with a) evolution of a stem with a distinct, small-celled, thick-walled cortex; b) a marked tendency for the leaves to become unlobed; c) an equally marked tendency—very unusual in *Lophocoleoideae*—for the leaves to be vertical and transversely oriented. Within the above complex of taxa, we find clear analogies to, especially, *Pachyglossa*. In *Pachyglossa* we also find brown-to-fuscous coloration in some taxa; microphyllous stolons; growth away from the substrate (in some taxa); and a combination of ventral and lateral-intercalary axillary branching with isolated *Frullania*-type branching, (depending on the species) rare or lacking. *Stolonophora*, however, is very distinct from the *Pachyglossa-Lophocolea boveana-australis-gunniana*

complex in the highly reduced and appressed underleaves, and the basically bilateral and two-ranked organization of vegetative axes.

KEY TO THE SPECIES OF *STOLONOPHORA*

1. Leaf margins not to weakly decurved, leaves pale to dark brown to red brown, leaf cells with walls moderately to distinctly thickened; axes 1.8-10.5 cm. tall; stems 185-335 μ in diameter; underleaves 0.15-0.35(-0.45) \times the stem width; perianth \pm included, for the most part sheathed by bracts; plants submerged in streams or pools or on stream banks. Southern South America *S. abnormis*.
1. Leaf margins tightly and narrowly revolute, leaves green, not developing secondary pigments, leaf cells with walls slightly thickened; axes 0.8-1.5 cm. tall; stems 150-170 μ in diameter; underleaves 0.40-0.55 \times the stem width; perianth exserted, bracts obliquely patent; plants on cliff walls subject to inundation. North and South Island, New Zealand *S. personii*.

1. ***Stolonophora abnormis* (Besch. & Mass.) Engel & Schust. *comb. nov.***

Leioscyphus (?) *abnormis* Besch. & Mass. Bull. Mens. Soc. Linn. Paris 1: 629, 1886. *Lophocolea abnormis* (Besch. & Mass.) Steph. Sp. Hep. 3: 62. 1906. *Clasmatocolea abnormis* (Besch. & Mass.) Grolle, Revue Bryol. Lichén. 29: 71. 1960. Type: Chile, Prov. Magallanes, Isla Hoste, *Hyades* (FH!, G!)(c. per.).

Plants gregarious with other bryophytes or in dense pure tufts; axes 1.8-10.5 cm. tall, the leafy shoots 0.5-1.1 mm. wide, pale to dark brown to yellow-brown, occasionally tinged with red-brown, stems red-brown or very dark brown, rather stiff, wiry.

Branches frequent, of lateral- and ventral-intercalary types, *Frullania*-type branching very rare (only 1 branch seen), leafy branches erect; stolons frequent but not uniformly present on all axes, pinkish tinted, often in an interwoven mass in which soil particles may be trapped, often prostrate from median or basal portion of leafy axis; stolons occasionally branched, with scaly leaves and underleaves which are sometimes caducous.

Stems 185-335 μ in diameter, 8-11 cells in diameter, cortex in 1-2 rows of very thick-walled cells the same size as or smaller than the medullary; the outer row with walls thickest and often with small lumen; medullary cells thin to slightly thick walled, with corners thickened similarly to small to medium trigones. Rhizoids absent from leafy shoots, common on stolons, at base of leaves and underleaves or occasionally stolons with a few regions of scattered rhizoids.

Leaves (fully developed) (0.7-)0.9-1.7 mm. wide, 0.7-1.3 mm. long, axes commonly with regions of small leaves intercalary between fully developed leaves; the later transverse to weakly succubously oriented, insertion narrow, transverse to distinctly succubous, leaves commonly subvertical, erect to weakly spreading, approximate to weakly imbricate, entire leaf weakly to moderately concave and with margins plane or leaves weakly to moderately concave in median portion but with peripheral portions nearly flat and with margins plane or slightly reflexed; leaves oblate to rotundate to ovate; apex broadly rounded to truncate, occasionally retuse.

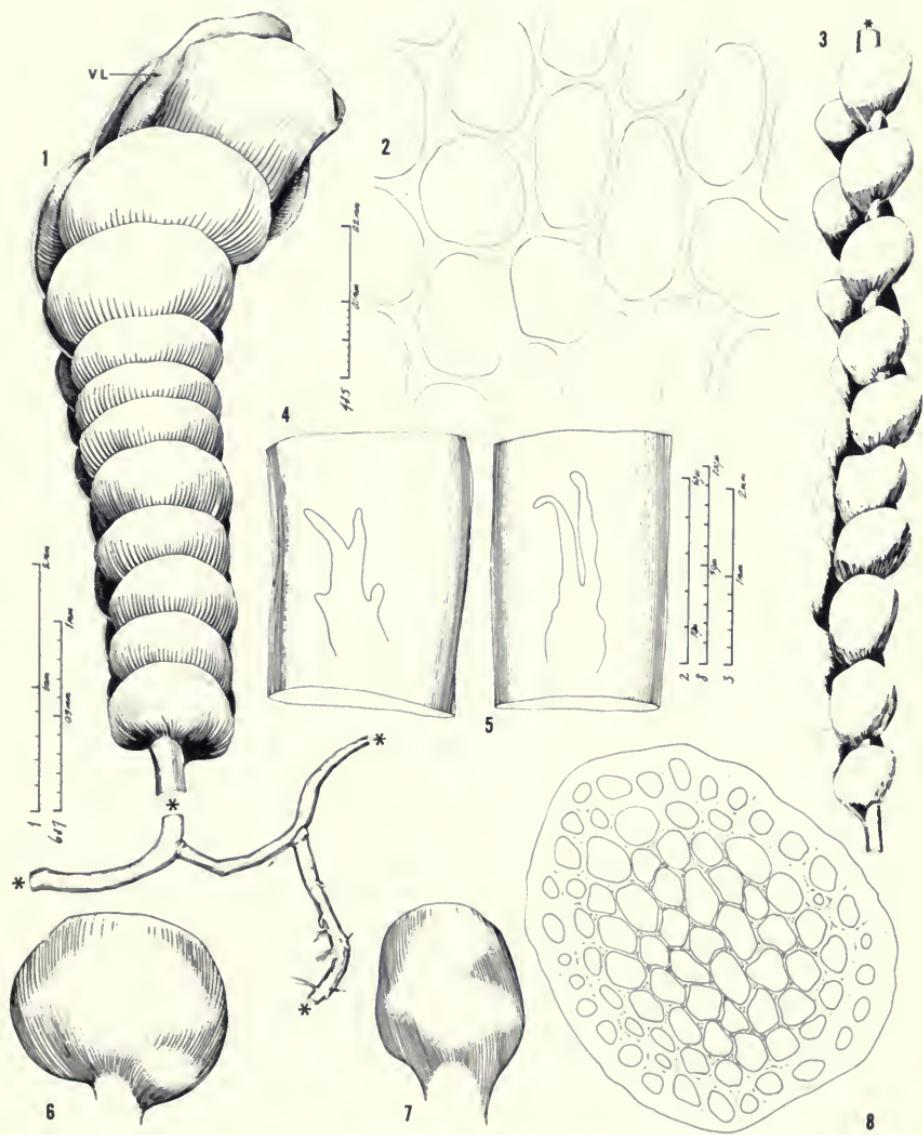


FIG. 1. *Stolonophora abnormis* (Besch. & Mass.) Engel & Schust. 1, perianth-bearing axis with basal stolons (VL = ventral lobe), $\times 16$; 2, median leaf cells, $\times 450$; 3, portion of leafy axis, $\times 11$; 4-5, underleaves of main, leafy axis, $\times 90$; 6-7, leaves of main axis, $\times 23$; 8, stem, cross-section through main, leafy axis, $\times 270$. Numbers 1, 4-6 from Engel 6092, Chile, Prov. Magallanes, Puerto Gallant; 2, 3, 7, 8 from type material.

Leaf cells with walls moderately to distinctly thickened, trigones medium to large, often confluent, the sides straight to bulging, occasionally concave; median leaf cells (12-)17-44 μ wide, (14-)26-53(-56) μ long, median basal cells distinctly thick walled, 18-42(-48) μ wide, (34-)41-76(-82) μ long; cuticle smooth or finely papillose.

Underleaves distinct, reduced, of very thick-walled cells, 0.15-0.35(-0.45) \times the stem width, moderately spreading; bifid to varying degrees and with segments ciliolate, or undivided and then acuminate, underleaf segments or apex terminating in a slime papilla; lamina margins entire or with 1 single-celled tooth.

Plants dioecious; δ bracts somewhat smaller than leaves, obovate to rotundate, moderately concave, margins plane, free margin of saccate portion often broadly rounded, entire, with 1 slime papilla or with 1-2 sharp teeth terminating in a slime papilla, bract otherwise entire; antheridial stalk uniseriate throughout or with isolated cells vertically septate.

Gynoecia on main axis or long lateral- or ventral-intercalary branches; subfloral innovations absent or from axil of bract of innermost series or bract or bracteole of second series, innovations often repeatedly producing perianths. Bracts in 2-3 series;

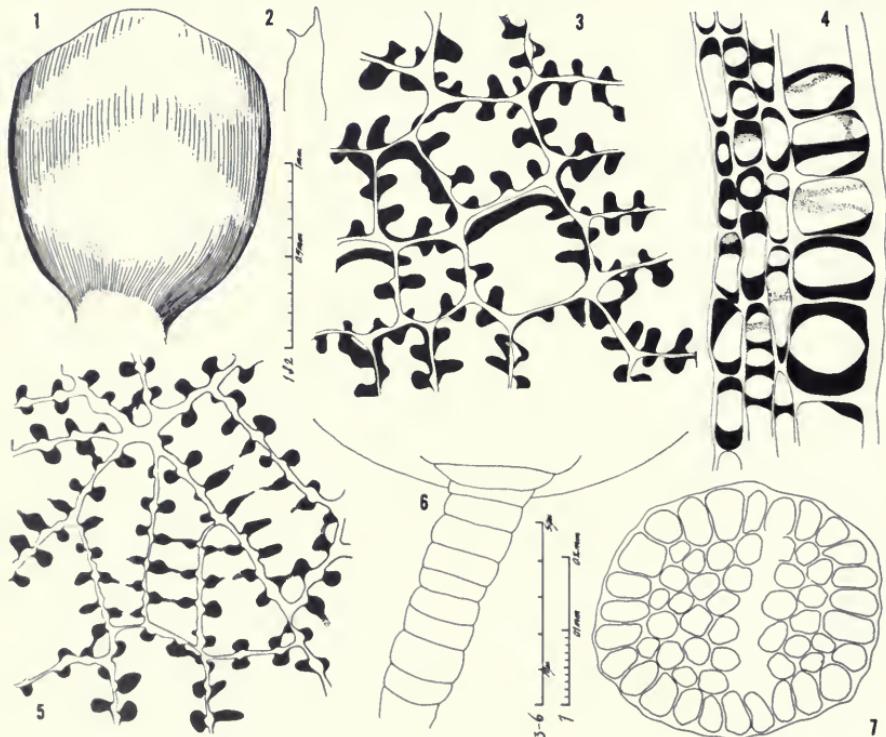


FIG. 2. *Stolonophora abnormis* (Besch. & Mass.) Engel & Schust. 1-2, bract and bracteole of innermost series, $\times 23$; 3, capsule wall, outer layer, $\times 450$; 4, capsule wall, cross-section, $\times 450$; 5, capsule wall, inner layer, $\times 450$; 6, antheridial stalk, $\times 450$; 7, partially torn seta, cross-section, $\times 90$. Numbers 1-5, 7 from Engel 6092, Chile, Prov. Magallanes, Puerto Gallant; 6 from Engel 5718, Chile, Prov. Magallanes, Bahía Tuesday.

bracts of innermost series free or with dorsal margin fused for entire length with perianth keel; deeply concave in median basal portion; rotundate to subrectangular to obovate, basal portion often \pm clasping perianth; apices broadly rounded to subtruncate. Bracteoles of innermost series free from bracts, rarely inserted on basal portion of perianth and then with 1 margin partially fused with perianth; bracteole highly reduced, 0.2-1.2 mm. long, hardly modified from underleaves; very short bifid or undivided and then with apices narrowly rounded or short to long apiculate, apex or segments terminating in a slime papilla; lamina margins entire or with several slime papillae and 1 to several small teeth terminating in a slime papilla. Perianth trigonous, clavate to \pm campanulate, somewhat laterally compressed, the sides convex, the ventral lobe convex to (more commonly) somewhat infolded, occasionally canaliculate; perianth expanding toward the mouth; the mouth wide or subconstricted, lobes broadly rounded, inflexed or occasionally straight in median portion and reflexed near the keels.

Seta 7-8 cells in diameter, with 25-28 rows of outer cells surrounding an inner core of scattered cells slightly to distinctly smaller than outer row and with corners thickened similarly to medium or large trigones. Capsule wall 32-48 μ thick, of 3-4 layers, outer layer of cells 2.2-3.6 \times as thick as each of interior strata, outer layer 16-26 μ thick, with red-brown thickenings on radial walls, the thickenings wide nodulelike to wide spinelike and often feebly tangentially dilated, with a few to several semiannular bands which are sometimes branched; inner layer of cells 7-8(11) μ thick, with light brown thickenings on radial and tangential walls, incomplete semiannular bands extending for varying lengths, bands only occasionally complete, nodulose and sharp spinose thickenings common. Spores 14-17 μ , light brown, exine with short, stout vermiculate ridges. Elaters 7-8(9) μ wide, bispiral to both ends or 1 or both apical portions with thick nonspiral walls, elater walls light brown.

The senior author has studied the spores of this species with the aid of a scanning electron microscope. Figures 3-4 reveal the spore exine is covered with short, stout, vermiculate ridges which are rather close to one another or often coalesce. It may be observed from Figure 4 that the ridges possess spherical nano-granules which are usually distinct and separate, with intervening spaces, but occasionally are juxtaposed or fused.

Ecology-Phytogeography.—*Stolonophora abnormis* occurs in Tierra del Fuego and the wet, cold Patagonian Channels north to 52° 17' S. The species occurs submerged in rather rapidly moving streams and occasionally on stream banks in evergreen *Nothofagus* forests or submerged in small pools in the Magellanian moorland. It may also be subalpine or alpine. It is also known from near Concepcion (ca. 36° 50' S in Prov. Concepcion) in the Valdivian region. Arnell (1958) reports the species from Tristan da Cunha.

Specimens seen.—CHILE. PROV. CONCEPCION: Peumo, Dusén 186 as *Jamesoniella paludosa* (S-PA). PROV. MAGALANES: Isla Pacheco, Skottsberg 141 as *Jamesoniella grandiflora*

(S-PA); Isla Desolación, Bahía Tuesday, at head of inner harbour, *Engel* 5697, 5718 (MSC); Isla Desolación, Puerto Churruga, at head of Brazo Lobo, *Engel* 5852, 5857 (MSC); Isla Desolación, Puerto Angosto, ca. 200 m., *Dusén* 186 as *L. abnormis* (G), as *Jamesoniella*



FIG. 3. *Stolonophora abnormis* (Besch. & Mass.) Engel & Schust. Scanning electron photograph of spore, $\times 7,500$; from *Engel* 6092.

paludosa (L, S-PA, UPS); NE side of Puerto Gallant, *Engel* 6065D, 6092 (MSC); Río Azopardo, ca. 500 m., *Dusén* 112 (G, S-PA); W end of Lago Fagnano, "alpinus," *Halle* 144, as *Jamesoniella oenops* (UPS); Isla Londonderry, *Exp. Ant. Belg.* 397 (G).

2. *Stolonophora perssonii* (Schust.) Engel & Schust. *comb. nov.*

Calyptrocolea perssonii Schust. *Revue Bryol. Lichén.* 34: 699. 1967.
Holotype: New Zealand, South Island, Fiordland Nat. Park, E

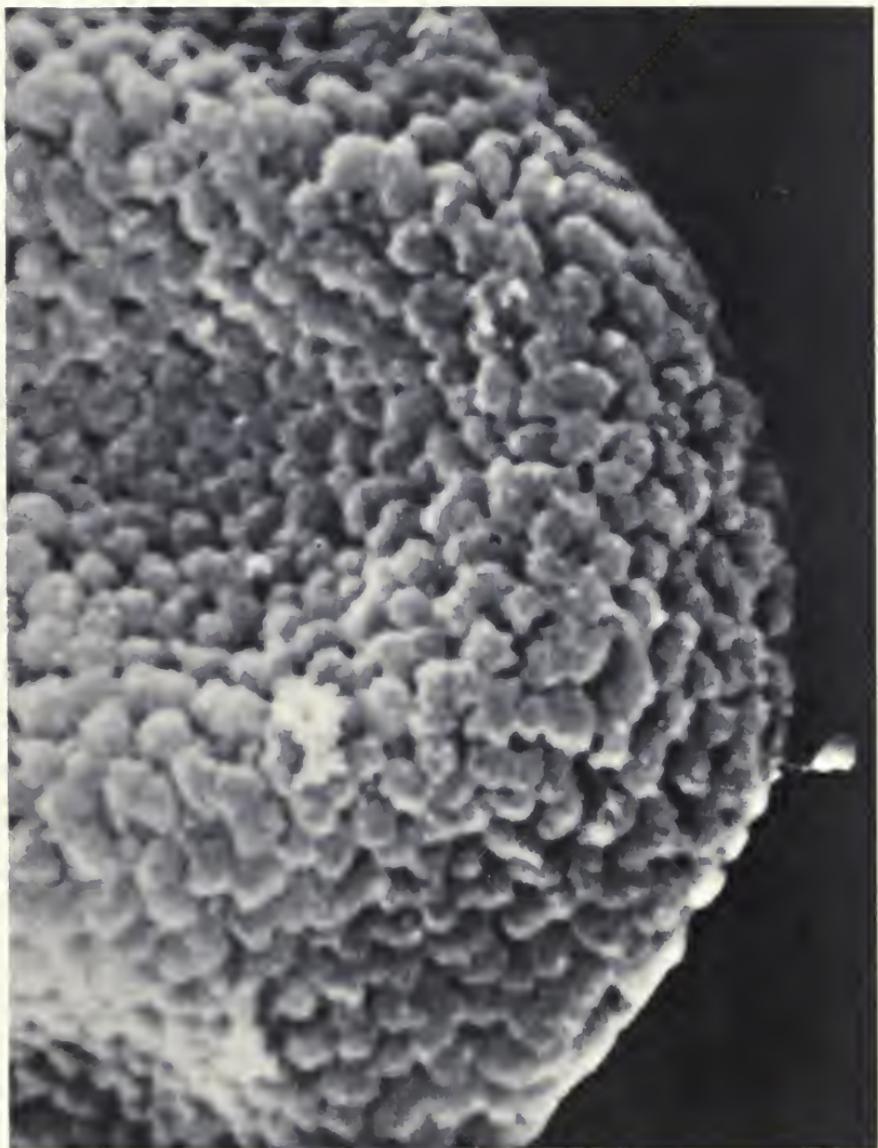


FIG. 4. *Stolonophora abnormis* (Besch. & Mass.) Engel & Schust. Scanning electron photograph of spore, $\times 14,350$; from Engel 6092. Details of exine showing ridges and nanogranules.



FIG. 5. *Stolonophora perssonii* (Schust.) Engel & Schust. 1, main axis, lateral view, $\times 23$; 2-3, abaxial (AB) and adaxial (AD) views of same main axis leaf, $\times 46$; 4-6, underleaves of main, leafy axis, $\times 90$; 7, dimorphic median leaf cells, with oil-bodies in some cells while absent in others, $\times 400$; 8, axis with stoloniform branching, ventral view (LA = leafy axis base), $\times 9$; 9, stem, cross-section through main leafy axis, $\times 270$. All from holotype.



FIG. 6. *Stolonophora perssonii* (Schust.) Engel & Schust. 1, shoot apex, ventral aspect, with barely emergent dehisced capsule, $\times 22$; 2, shoot apex with perianth, dorsal aspect, $\times 22$; 3, shoot sector, dorsal aspect, with lateral-intercalary branch, $\times 31$; 4, shoot sector, lateral aspect; note appressed underleaves, $\times 31$; 5, female bract and, within, bracteole, to one scale, $\times 22$; 6, bracteole of Figure 5, $\times 375$; 7, leaf, $\times 31$; 8, capsule wall, outer layer, $\times 312$; 9, capsule wall, inner layer, $\times 312$; 10, capsule wall, cross-section, $\times 500$; 11, portion of plant showing highly ramified base; arrows indicate points of removal of leafy shoot apices; note branches x, y, z, from all three merophyte rows of the primary axis, $\times 44$. Numbers 1-10 from Schuster 48872, New Zealand, Mt. Egmont; 11 from holotype.

entrance of Homer Tunnel, head of Hollyford Valley, 3000-3050 ft., *Schuster 55596 (RMS!)*.¹

Plants in nearly pure, rather dense tufts; axes 0.8-1.5 cm. tall, the leafy shoots ca. 0.7-1.2 mm. wide, subequally leaved throughout, green to slightly olive green, with the mature stem brownish.

Branches frequent, intertwined, of lateral- and ventral-intercalary types, the ventral-intercalary more common, terminal branching absent, leafy branches erect; stolons frequent, usually pinkish tinted, often descending or prostrate from base of leafy axis; stolons often branched, with scaly, often hyaline leaves and underleaves which are sometimes caducous.

Stems ca. 150-170 μ in diameter, 9-11 cells in diameter, cortex in 1-2 rows of very thick-walled cells smaller than the medullary; medullary cells thin walled, with corners thickened similarly to small trigones. Rhizoids rather frequent, on leafy shoots restricted to underleaf bases; on stoloniform axes at bases of leaves and underleaves.

Leaves 0.6-0.85(-0.9) mm. wide, 0.6-0.7 mm. long, transverse to subsuccubously oriented, insertion narrow, weakly to distinctly succubous, leaves subvertical, moderately to rather strongly spreading, distant to weakly imbricate, moderately concave in median portions, the peripheral portions nearly flat, but with margins narrowly, often strikingly reflexed; leaves rotundate; apex broadly rounded to truncate to weakly retuse.

Leaf cells with walls slightly thickened, trigones medium, occasionally confluent, the sides concave to straight; median leaf cells 13-20 μ wide, 22-29(-37) μ long, median basal cells uniformly and moderately thick walled, elongated, 13-20 μ wide, 22-29(-37) μ long; cuticle smooth. Cells dimorphic: a majority each with 2, extremely rarely 3 oil-bodies, a minority of 10-20 per cent without oil-bodies; oil-bodies colorless, faintly granulate, almost smooth externally, subspherical to ovoid, ca. 3-5 \times 5-8 μ or spherical and 4-5 μ .

Underleaves distinct, reduced, 0.40-0.55 \times the stem width, appressed; with 1-2 often cilialike segments or undivided.

Plants dioecious; δ bracts hardly smaller than leaves, ovate to rotundate, deeply concave, margins reflexed, entire; antheridial stalk uniserrate but with local biseriate areas.

Gynoecia terminal on leading axes; subfloral innovations absent. Bracts in 3 series; bracts of innermost series rather stiffly obliquely patent, deeply concave to cupulate, especially toward median base; rotundate, essentially identical to leaves in size and shape; apices narrowly revolute to decurved, broadly rounded; margins distally narrowly revolute to decurved. Bracteoles of innermost series free from bracts; minute, at most 0.05-0.1 area of bracts; appressed. Perianth often rather stipitate, clearly exserted, obovoid to ovoid, inflated-trigonous, the 2 lateral keels locally weakly winged and \pm sharp, the dorsal keel blunt to rounded; slightly contracted to the shallowly trilobed mouth, lobes blunt to rounded, margins reflexed.

Seta 8-9 cells in diameter, with 31-32 rows of outer cells surrounding an inner core of scattered cells subequal to or slightly larger than outer row and with corners

¹ The acronym RMS indicates the private herbarium of R. M. Schuster.

thickened similarly to medium trigones. Capsule spherical, wall 32-40 μ thick, of 4(-5) layers, outer layer of cells 2.8-3.7 \times as thick as each of interior strata, outer layer 17-18 μ thick, with thickenings on radial walls, the thickenings wide nodulelike to wide spinelike; inner layer of cells 5-6 μ thick, with weak nodular thickenings on radial walls, thickenings rarely tangentially dilated, semiannular bands rare to sporadic, usually incomplete. Spores 12-14 μ , light brown, exine rather thin and with low vermiculate, close, irregular anastomosing ridges. Elaters 8-10 μ wide in median portion, medially mostly 3-spiral, becoming bispiral distally, spirals very narrow.

Taxonomic remarks.—This species was treated by Grolle (1972, p. 365) as a synonym of *Clasmatocolea fiordlandiae* (Hodgs.) Grolle. *Clasmatocolea fiordlandiae*, type material of which has been studied by the senior author, rightfully belongs to *Clasmatocolea* and is not conspecific with *Stolonophora perssonii*. For notes regarding generic differences between *Stolonophora* and *Clasmatocolea* see p. 113.

Schuster (1967, p. 700) assigned this species to *Calyptrocolea* (thus the Adelanthaceae) and placed it there because it is exceedingly close in habit to *Calyptrocolea gemmipara* Schust. However, he noted that the position of "C." *perssonii* in "*Calyptrocolea* is subject to possible doubt" and noted that it differed from *C. gemmipara*, in "a series of good vegetative characters," i.e.: the dimorphic leaf cells; the thick-walled cortical cells that are short-oblong rather than long-rectangular; the occasional lateral-intercalary branches; and the distinct, if small underleaves. The near-identity of the two taxa in size, stolons, leaf form and orientation, plus the absence of terminal branching, is truly astonishing. Study of the antheridial and perianth-bearing plants we have seen clearly shows that the species rightfully belongs in the Geocalycaceae.

The name "*Calyptrocolea dimorpha*" in Schuster (1966, p. 211) is actually an herbarium name for *C. perssonii*.

It should be specifically mentioned that *S. perssonii* has dimorphic leaf cells, i.e., some leaf cells possess oil-bodies while others are totally oil-body free (see fig. 5). This situation is rather exceptional in the Hepaticae and occurs in several unrelated taxa (cf. Schuster, 1966).

Ecology-Phytogeography.—*Stolonophora perssonii* is known only from limited materials. It is an alpine species and occurs on cliff walls subject to inundation, adjacent to steep cascades and small waterfalls at 3000-3050 ft. in Fiordland National Park, South Island, New Zealand, and at similar sites at 5000-5400 ft. on Mt.

Egmont, North Island, New Zealand. It may be associated with *Temnoma quadrifidum*.

Specimen seen.—NEW ZEALAND. TARANAKI PROV.: Mt. Egmont, east slope of mountain near Warwick Castle in alpine summit zone, 5000-5400 ft., Schuster 48872 - c. ♂ + sporo. (RMS).

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